

Research Article

Short-Term Plant Community Responses to Warming and Defoliation in a Northern Temperate Grassland

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Little is known about the short-term impacts of warming on native plant community dynamics in the northern Canadian prairies. This study examined the immediate effects of elevated temperature and defoliation on plant community diversity, composition, and biomass within a native rough fescue (*Festuca hallii* (Vasey) Piper) grassland over two growing seasons. We used open-top chambers to simulate climate change and defoliated vegetation in midsummer of the first year to simulate biomass loss associated with periodic ungulate grazing. Warming marginally increased plant species diversity and changed community composition shortly after treatment, but effects were not apparent the second year, and there were no apparent impacts on plant biomass. Nonetheless, warming may have impacted community diversity indirectly through reduced soil moisture content, a pattern that persisted into the second year. Overall, this northern temperate grassland demonstrated limited community-level changes to warming even in the presence of defoliation.

1. Introduction

Over long time scales, the plant community composition within savanna habitats is sensitive to climate change [1, 2]. Over the past 50 years, western Canadian savannas, such as the Aspen Parkland ecoregion, have experienced an increase in mean annual temperature of approximately 1.3°C [3]. Mean temperatures for this region are predicted to further increase over the next century, leading to higher evaporation rates and reduced soil moisture availabilities [4, 5], as well as a longer frost-free period [6]. The consequences for native vegetation within these regions are unclear.

Under anticipated climate change scenarios, native savanna ecosystems, existing as a mosaic of community types, may be particularly prone to ecological change [7]. Moreover, land-use practices such as livestock grazing may

exacerbate any climate-driven changes in vegetation [8]. Plant community changes arise when species vary in their fundamental response to environmental and management factors, including temperature and defoliation in the form of grazing. Warming can impact plants both directly by altering the potential for photosynthesis throughout the growing season [9] or indirectly by altering complex secondary biological processes in the ecosystem [10]. Collectively, warming and defoliation may lead to reductions in the diversity of native species or the invasion of undesirable species [11].

The Aspen Parkland of western Canada is historically a distinct savanna habitat comprised of a mosaic of forest and grassland communities. Currently, few native grasslands persist in the region [12] due to human land-use practices, making ecosystems in this region one of the most threatened in western Canada. Plant communities in the Aspen Parkland

are known to have varied greatly over time [1], presumably due to the marked impact of ongoing fluctuations in climate coupled with secondary disturbance [13]. Plant growth in this region is typically limited by low temperatures during winter and spring and by water stress during late summer [5], but recent projections suggest that the Aspen Parkland may expand by as much as 21% due to climate change [14].

Grazing by large ungulates is both historically and currently a common disturbance in grasslands of the Aspen Parkland [15, 16]. Removal of plant biomass may exacerbate soil warming through reduced shading of the soil surface and altered soil moisture availability [17]. Moreover, warming and defoliation induced changes to plant growth and associated litter biomass may further impact plant community composition, including plant species diversity [18]. Ultimately, there is reason to suspect that nonadditive effects may exist between the disturbances of warming and defoliation, with the magnitude of final changes dependent on whether plant species adapted to one stressor are adapted to the second.

Climate change and the associated changes in growing conditions (e.g., moisture availability) have been widely implicated for their potential to negatively affect agricultural ecosystems [19]. Thus, investigation of the impact of elevated temperatures in conjunction with grazing as the prevailing land use will improve our understanding of the response of these ecosystems to climate change. To understand and mitigate the potential impacts of climate change on the biodiversity and sustainable production of Canada's remaining native Parkland grasslands, a mechanistic understanding is needed of the relationship between temperature and defoliation within these areas.

We examined the immediate impacts of warming, with and without defoliation, on plant community composition, diversity, and biomass, within a native rough fescue grassland in the Aspen Parkland of Alberta, Canada. Moreover, we predicted that defoliation would augment the impacts of warming with the removal of litter, as the latter is known to be an important driver of plant growth in these grasslands [20]. We also examined how plant community characteristics were associated with key abiotic environmental variables, including light availability, soil moisture content, soil nitrogen mineralization rates, and soil temperature.

2. Materials and Methods

2.1. Field Site. We conducted a field experiment within a native rough fescue grassland in the Aspen Parkland natural subregion of Alberta, Canada, in 2006 and 2007. The study was conducted in a 20 ha area at the University of Alberta Kinsella Research Station (53°05'N; 111°33'W), situated 150 km southeast of Edmonton. The area climate is dry subhumid, with mean annual precipitation of 431 mm and mean annual temperature of 1.5°C [20]. Mean annual growing season (May–September) precipitation over the past 30 years was 312 mm, with mean annual growing season temperature of 13.9°C. In 2006 and 2007, annual growing season precipitation was 269 and 287 mm, respectively;

although below the 30-year norm, these conditions are not unlike those of the last decade during which growing season precipitation averaged 284 mm [21]. Mean annual growing season temperature was 16.1°C in 2006, 2.2°C warmer than in 2007 (13.9°C).

Dominant grasses at the study site included *Hesperostipa curtiseta* (A.S. Hitchc) Barkworth, *Festuca hallii* (Vasey) Piper, *Koeleria macrantha* (Ledeb.) Schult., and dryland *Carex* species. Dominant forbs included *Achillea millefolium* L., *Commandra umbellata* L., *Aster falcatus* (Lindl.), *Artemisia ludoviciana* (Nutt.), and *Solidago missouriensis* (Nutt.). *Rosa arkensana* (Porter) was also prevalent [22]. A more detailed description is available in Lamb [18].

Soils at the study site are Dark Brown Chernozems and are generally well drained. On average, soils are loamy in texture (22% clay, 33% silt, and 45% clay) have a pH of 5.7, Ah depth of 13.1 cm, and approximately 13% organic matter. Although the dominant native vegetation found at this site has been characterized as deep rooted [23], most root biomass in the study area remains situated within 20 cm of the ground surface as rocks and hard packed clay limit the ability of roots to reach lower depths [24]. While the study area had a long history of fall grazing by cattle, it had not been grazed for 3 years prior to the start of this study.

2.2. Experimental Design. The experiment was established in a randomized complete block design with five replicate blocks each 5 × 5 m in size. Each block was more homogeneous with respect to soil type, slope, aspect, and drainage than between blocks. Within each block, four 2 m diameter circular plots were established and four treatment combinations were randomly assigned. Treatments included a control, warming, defoliation, and warming + defoliation.

We used open-top chambers (OTCs) situated directly over the plots to increase air temperatures. The OTCs are a low-cost, proven method to increase air temperature in field studies [25] with previous studies demonstrating an increase of 1 to 2°C in average daily temperature [26, 27]. Our OTCs were 40 cm high and cone shaped, with 2 m diameter at the bottom and 1.6 m diameter at the top (Figure 1). The OTCs were made from Sunlite HP solar glazing material (Solar Components Corporation, Manchester, NH, USA), which allows visible light transmission but reradiates light in the infrared range, creating a greenhouse effect within the OTC. OTCs were placed on the plots in April right after snowmelt and removed in October after the current years growth had senesced. Initial data collected in June 2006 indicated that this design provided an increase of up to 4°C in air temperature near midday, although average daytime temperature increases were closer to 1.6°C.

Defoliation was achieved through manual clipping of all standing vegetation in and around each plot (including a 50 cm nonsampled buffer). Clipping was done in mid-June 2006 to a stubble height of 2.5 cm above ground and is consistent in timing and intensity with the common land-use practice of midsummer cattle grazing across the region. Although actual ungulate grazing would have been more representative of the disturbance these communities experience,



FIGURE 1: Close-up of an open-topped chamber (OTC) used to increase temperature within warmed grassland plots.

ungulates could not be used due to their tendency to feed in a spatially heterogeneous (i.e., patchy) manner as well as pose risk of damaging OTCs. Defoliation was not done in 2007 in order to examine the residual impacts of defoliation during the previous year and assess community recovery from grazing under both warmed and unwarmed conditions.

2.3. Vegetation Sampling. Plant community composition in each plot was assessed in early August 2006 and 2007 within a centrally located 0.5×0.5 m quadrat. Percent canopy cover for each species was visually assessed in each quadrat, from which we calculated plant species richness (number of species) and Shannon's diversity index as

$$H' = \Sigma(P_i * \ln P_i), \quad (1)$$

where P_i is the proportion of total species cover comprised of each individual species " i ." Shannon's diversity was used as it accounts for both the relative abundance and density of plant species in a plot.

Destructive biomass sampling occurred within a separate 0.25×0.5 m area within each plot at peak biomass (early August) of each year, within which total live shoot biomass was sorted from plant litter. Root cores (5 cm wide $\times$ 20 cm deep) were also removed from each quadrat at the time of harvest to assess root biomass at the community level [28]. Only one core was removed from each plot due to limited space for destructive sampling. Cores were washed free of soil through a 0.5 mm sieve. Both above and below ground vegetation samples were dried at 65°C to constant mass and weighed.

2.4. Environmental Sampling. To determine the predominant environmental factors that were influenced by our experimental treatments and associated with community composition, we measured several parameters during the growing season. Air temperatures were recorded every 10 minutes in the summer of 2006 within warmed and unwarmed plots using Boxcar HOBO data loggers (Hobo H8 Pro Series, Onset Computer Co. Procasstet, Mass, USA) installed in PVC radiation shields 2 cm above ground level. Temperatures were averaged daily, as well as from 0600 until 1800 hr to assess daytime air temperatures within each plot.

Soil moisture and temperature readings were taken 4–7 days after rainfall in both June and July, near midday to assess treatment-induced differences in the microenvironment under field conditions. Moisture content was measured in the top 10 cm of mineral soil using a TDR-MLX2 moisture probe (Delta-T Devices, Cambridge, UK), with a minimum of 4 replicate measurements per plot in each of 2006 and 2007; measurements were then averaged to obtain a per plot estimate of moisture content.

Light interception by vegetation was measured coincident with soil moisture content using a Li-Cor ceptometer (Li-Cor Inc, Lincoln, Neb, USA) and reported as photosynthetically active radiation (PAR). Values of PAR were measured above and below the vegetation canopy using an average of 10 segmented sensors to assess light penetration to the soil surface. Readings were taken in the center of the plot and outside the shading influence of the OTC. The proportion of light intercepted was then calculated using the following equation:

$$\left[\frac{(\text{above canopy PAR} - \text{below canopy PAR})}{\text{above canopy PAR}} \right] * 100\%. \quad (2)$$

In order to assess *in situ* net nitrogen mineralization rates, the buried-bag method [29] was used. Duplicate soil cores (5 $\times$ 15 cm) were taken monthly at 0–5 cm depth and combined for subsequent analysis. Additionally, N supply rates were measured monthly during 2007 using Plant Root Simulator (PRS) probes (Western Ag Innovations Inc, Saskatoon, SK, Canada). Detailed methods are provided by Attaeian [30].

2.5. Data Analysis. To examine the impact of warming on the microenvironment of plots prior to plant responses, we conducted separate general linear mixed models using the June 2006 (the start of the experiment) measures of soil moisture and light interception as response variables. In each analysis, the presence or absence of an OTC served as the fixed effect, with block as a random factor. Soil temperature was tested in July 2006 after soil temperatures were assumed to have equilibrated with the presence of the OTCs. Analyses were conducted using Proc Mixed in SAS 9.1.3 (SAS Institute Inc., Cary, NC, USA).

To test the impact of warming and defoliation on plant community structure, a permutation-based MANOVA (perMANOVA) [31] and a multi-response permutation procedure (MRPP) [32] were run using a Sorenson distance measure on the community composition data for August 2006 and 2007 in PC-ORD version 5 (MJM Software Design, Gleneden Beach, Ore, USA). For the perMANOVA, 4999 randomizations were used and significance was based on the proportion of randomized trials with an indicator cover greater than or equal to the observed cover value, such that

$$P = \left[\frac{(1 + \text{number of runs} \geq \text{observed})}{(1 + \text{number of randomized runs})} \right]. \quad (3)$$

For the MRPP, significance was based on the probability of the observed delta statistic being smaller or equal to the expected delta.

To further examine plant species responses to the warming treatment, a nonmetric multidimensional scaling (NMS) [33, 34] ordination was run on vascular plant cover data from early August in both 2006 and 2007 using a Sorensen distance measure in PC-ORD. Real data were run 250 times, as were the randomized data for the Monte Carlo test. A total of 500 iterations were used to obtain the final stable solution with instability of 0.00001. Axes scores were interpreted based on Pearson and Kendall correlations with all species found across the site. An indicator species analysis [35] using 4999 permutations was also performed on the August 2006 community data to examine specific plant species responses to warming.

To test the impact of warming and defoliation on overall plant species diversity and biomass, general linear mixed models were run on August 2006 and 2007 measures of plant species richness, diversity, and shoot, litter, and root biomass. We used an alpha of 5% to indicate significance and minimize the potential of a type II error, although relationships with an alpha of 10% were also examined.

Finally, to identify abiotic variables associated with variation in community composition, Shannon's diversity (plant species), and biomass, we performed a series of multiple regression analyses that included soil temperature and moisture content, *N* mineralization rates, and light interception from the preceding two months (June and July) within each year as independent factors. A stepwise multiple regression was used with the minimum significance level of entry into the model set at 10%.

3. Results

3.1. Microenvironment and Relation to Vegetation. The OTCs had the anticipated effects on abiotic conditions, increasing daily surface air temperatures by 1.0°C and average daytime air temperatures by 1.6°C during 2006. Warming did not impact soil temperature in July 2006 ($F_{1,12} = 0.12$, $P = 0.73$), but showed a potential impact on June 2006 soil moisture content ($F_{1,14} = 3.78$, $P = 0.07$), with warmed plots drier ($24.7 \pm 1.4\%$) than unwarmed plots ($26.7 \pm 1.4\%$). There was no evidence that the OTCs altered light interception by vegetation in June 2006 ($F_{1,14} = 0.97$, $P = 0.34$), with warmed plots ($31.8 \pm 2.7\%$) similar to unwarmed plots ($28.9 \pm 2.7\%$).

Environmental variables showed a minor relationship with vegetation during both years of the study, with the strongest association between soil moisture content and the plant community, particularly Shannon's diversity and richness (Table 1). Additionally, shoot biomass was significantly related to light interception (Table 1).

3.2. Influence of Warming. Our perMANOVA analyses of plant community composition revealed a weak effect of warming in 2006 (perMANOVA pseudo- $F = 2.10$, $P = 0.07$; MRPP $A = 0.021$, $P = 0.12$). The 2006 NMS also indicated

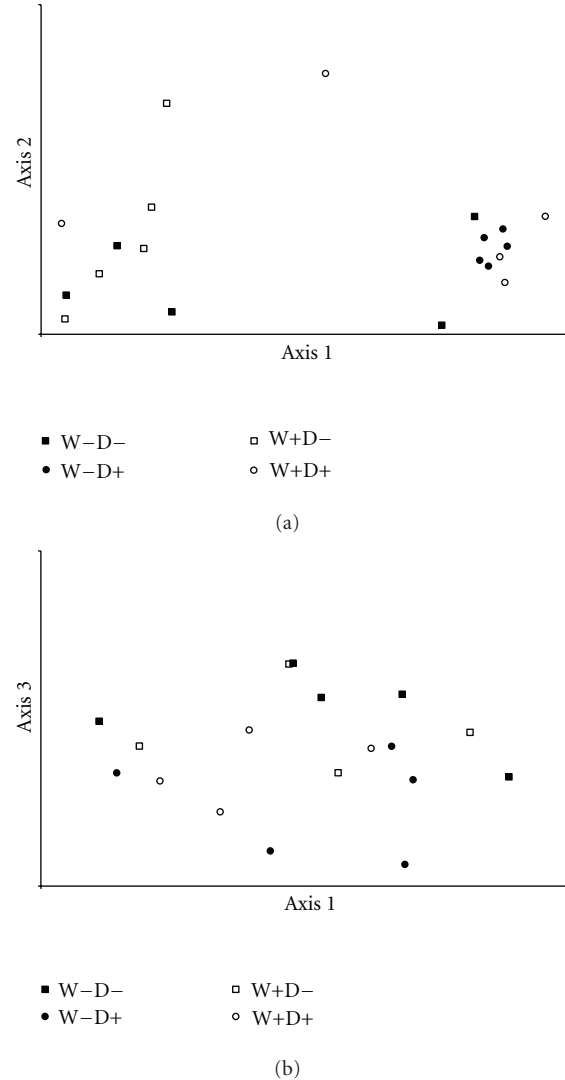


FIGURE 2: Distribution of plots based on an NMS ordination of plant community cover data sampled in either (a) August 2006 or (b) August 2007. Treatments are warmed (open symbols) and nonwarmed (solid symbols), and nondefoliated (square) and defoliated (circle).

an effect of warming on community composition, however, with Axis 1 showing evidence of groupings of plots based on the warming treatment (Figure 2(a)). NMS Axis 1 was closely associated with *Hesperostipa curtiseti* ($r = -0.82$), *Koeleria macrantha* ($r = -0.60$), and *Artemisia frigida* ($r = -0.54$) ($P < 0.05$), with results further confirmed in the indicator species analysis through the response of *K. macrantha* ($P = 0.05$) and *A. frigida* ($P = 0.10$) to warming. The 2006 NMS analysis resulted in a two-dimensional final ordination solution (Axis 1: $P = 0.004$, Axis 2: $P = 0.004$), with final stress of 10.34. The proportion of species variance represented by Axis 1 was 65.6% and by Axis 2 was 24.1%, based on the correlations between ordination distances and distances in the original n -dimensional space.

By 2007, there was no evidence of any lasting effect of warming on community composition, regardless of the

TABLE 1: Stepwise multiple regression models relating plant species diversity, biomass, and community composition, as well as NMS plot scores to measured environmental variables (soil temperature, soil moisture content, light interception, and nitrogen mineralization rate).

Year	Dependent Variable	Model R^2	Independent variable	Partial R^2	Beta _i	Prob > F
2006	Species diversity	0.59	Light interception (July)	0.19	0.01	0.09
			Soil moisture content (June)	0.27	0.06	0.02
			N mineralization (July)	0.13	-0.19	0.08
	Species richness	0.43	Soil moisture content (June)	0.43	0.47	0.006
	Shoot biomass	0.28	Light interception (June)	0.28	38.94	0.03
	Root biomass	0.30	N mineralization (July)	0.30	33.53	0.03
	NMS Axis 1	0.22	Light interception (July)	0.22	0.009	0.07
	NMS Axis 2	0.51	Soil moisture content (June)	0.38	0.11	0.01
			Soil temperature (July)	0.14	0.15	0.08
2007	Species diversity	0.19	Soil moisture content (July)	0.19	0.05	0.05
	Species richness	0.35	Soil moisture content (July)	0.35	0.72	0.006
	Shoot biomass	0.27	Light interception (July)	0.27	24.19	0.02
	Root biomass	0.59	Light interception (July)	0.35	-246.1	0.006
			Soil moisture content (June)	0.24	1090	0.006
	NMS Axis 1	—	None	—	—	—
	NMS Axis 2	0.27	Soil moisture content (June)	0.27	0.11	0.02
	NMS Axis 3	—	None	—	—	—

methods of analysis used (perMANOVA pseudo- $F = 0.91$, $P = 0.52$; MRPP $A = -0.006$, $P = 0.64$). The 2007 ordination with NMS also showed no distinct patterns associated with the warming treatment (Figure 2(b)). The 2007 NMS resulted in a three-dimensional final ordination solution (all axes $P = 0.004$), with final stress of 10.26. Axis 1 represented 27.2% of the variance, while axis 2 represented 5.6% and Axis 3, 56.2%.

Direct impacts of warming were found through a general linear mixed model on Shannon's species diversity, but only in 2006 ($F_{1,12} = 4.68$, $P = 0.05$), during which warmed plots ($H' = 1.91 \pm 0.11$) were more diverse than unwarmed plots ($H' = 1.69 \pm 0.11$). In contrast, warming showed no impact on species richness, shoot biomass, root biomass, or litter biomass (Table 2).

3.3. Influence of Defoliation. Defoliation strongly affected plant community composition in 2006 (perMANOVA pseudo $F = 6.62$, $P = 0.0006$), though these effects also did not carry over into 2007 (pseudo $F = 0.78$, $P = 0.64$). The lack of a warming by defoliation interaction in 2006 (pseudo $F = 0.55$, $P = 0.77$) and 2007 (pseudo $F = 0.82$, $P = 0.62$) indicated that the effects of defoliation on community composition were not dependent on warming.

Defoliation impacted species diversity and peak shoot biomass in 2006, as well as peak shoot and litter biomass in 2007 (Table 2). Species diversity was lower in the defoliated plots ($H' = 1.61 \pm 0.12$) compared to the nondefoliated plots ($H' = 2.00 \pm 0.11$). Total (accumulated) season-long shoot biomass was 25% greater in defoliated plots ($259.2 \pm 20.3 \text{ g m}^{-2}$) compared to non-defoliated plots ($206.7 \pm 20.3 \text{ g m}^{-2}$) in 2006. However, defoliated plots remained 19% lower in shoot biomass relative to non-defoliated plots in 2007 (199.6 ± 17 versus $246.1 \pm 17 \text{ g m}^{-2}$, resp.), the year

of no defoliation. Despite this, no interaction of warming with defoliation was found on any of the response variables, including species richness, peak shoot biomass, peak root biomass, and litter biomass in either year of the study (Table 2), again indicating that warming did not alter the response of plants to the defoliation treatment.

4. Discussion

Warmer conditions produced by the OTCs ($\sim 1.6^\circ\text{C}$ in daytime) were similar to the increases in mean annual air temperature seen in western Canada over the past 50 years [4, 36] and reinforce the utility of this method of imposing a modest increase in air temperature for examining the biological consequences of climate change. The observed reduction in soil moisture availability associated with the warming treatment suggests either that the OTCs indirectly reduced ambient rainfall into plots or, more likely, that the modest increase in temperature increased evapotranspiration. While limited in magnitude, the reduction in measured soil moisture availability (by 5.4%) provides support to the notion that a warmer microenvironment may increase the potential for water stress in this northern temperate grassland and could also explain why some climate change models [14] predict a shift northward in the boundaries of the Aspen Parkland. However, this observation must be tempered by the fact that rainfall was below normal during the study period and must therefore be interpreted in this context. Although it is important to recognize that temperature fluctuations, both seasonally and interannually, are typical of most grasslands, to which this is no exception, making it possible that the increase here was within the normal range of variation for this ecosystem, growing conditions during the two study years examined

TABLE 2: Summary of ANOVA results (F and $\text{Prob} > F$ values) for type III tests of fixed effects of warming, defoliation, and their interaction on plant diversity and biomass in 2006 and 2007. The F and $\text{Prob} > F$ values are highlighted when $\text{Prob} > F$ is less than 0.05.

Year	Variable	Df (Num, Den)	Warming (W)		Defoliation (D)		$W * D$ interaction	
			F -value	$\text{Prob} > F$	F -value	$\text{Prob} > F$	F -value	$\text{Prob} > F$
2006	Species richness	1, 12	1.36	0.27	0.87	0.37	1.96	0.19
	Species diversity	1, 12	4.68	0.05	13.61	0.003	2.19	0.16
	Shoot biomass	1, 12	1.74	0.21	10.82	0.006	0.00	0.97
	Root biomass	1, 12	0.88	0.37	0.27	0.61	0.04	0.84
	Litter biomass	1, 16	1.48	0.24	0.92	0.35	0.06	0.81
2007	Species richness	1, 12	0.02	0.88	2.78	0.12	0.02	0.88
	Species diversity	1, 12	0.14	0.72	0.42	0.53	0.53	0.48
	Shoot biomass	1, 12	0.01	0.91	3.98	0.07	0.26	0.62
	Root biomass	1, 16	0.28	0.60	2.38	0.14	0.33	0.57
	Litter biomass	1, 12	1.17	0.30	11.05	0.006	0.00	0.98

here remained consistent with recent climatic trends for the Aspen Parkland, which has experienced an increased frequency of summer drought during the 1990s [5].

Warming had a limited impact on plant community composition immediately following its initiation, but impacts were not apparent in the second year of study. The marginal increase in diversity rather than richness under warming in 2006 suggests that the combination of increased temperature and lower soil moisture favored the development of a more even plant community rather than a greater number of species. Richness is often slower to respond than Shannon's diversity, as the former entails a change in the absolute presence of individual plant species. Several plant species, including *H. curtipetala*, *K. macrantha*, and *A. frigida*, showed evidence of an initial positive response to warming in our study. Notably, these species are common dominants of grasslands across the Mixed-grass Prairie region to the south of the Aspen Parkland [37] and a shift in dominance to such species could suggest a potential change in prairie structure under warmer and potentially drier conditions. Niu and Wan [38] documented changes in plant competitive hierarchy arising from differential responses to warming in northern China and may account for some of the short term changes observed here.

Plant shoot and root biomass representing the entire plant community appeared resistant to the influence of warming in the short-term. Given that changes in aggregate community biomass are unlikely to be seen until reductions in vigor occur within plants, changes in biomass may be expected to take much longer than two years to develop. Nonetheless, this does not discount potential changes in biomass of individual species. For example, working in wet meadows of northern Alaska, Hollister and Flaherty [39] found an increase in sedge biomass under 1-2°C warming, but similar to our findings total community biomass did not change. In the present study, warming also failed to interact with defoliation to alter plant composition or biomass production, suggesting that warming induced by the OTCs did not influence tolerance of this community to defoliation, including recovery the following year. In general, defoliation had a more acute and consistent impact on the plant

community, leading to immediate reductions in diversity as well as extended declines in biomass production.

In general, few studies exist to directly compare our results to, particularly given that no studies have examined the direct effects of warming on northern temperate grasslands dominated by cool season plant species. Nevertheless, our results indicate that defoliation (i.e., the predominant land use in the area) has a greater immediate impact on Parkland grasslands than warming and is consistent with projections of global biodiversity responses for terrestrial ecosystems by others [11]. These same authors, however, suggested that northern temperate ecosystems may experience the least biodiversity change in the future, largely due to the acute changes already produced by previous changes in land use activities [11]. Our results provide at least some evidence that contrasts this perspective, as warming of Parkland grasslands did induce changes in species composition, albeit minor and potentially short lived. Interpretation of defoliation impacts must also be placed in the context of the clipping treatments imposed rather than the use of grazing animals. As animals are selective during defoliation and have significant impact on soils (e.g., through compaction and nutrient cycling), the impacts of large herbivores under warming may differ from the current results in these landscapes. More research is needed on these questions in this region of North America.

Long-term studies are recommended to more definitively establish the mechanisms behind the observed changes in species composition, particularly those xeric adapted plant species. For example, community dynamics in this study were associated primarily with light and soil moisture availabilities rather than soil temperature. This observation suggests that the predominant driver of climate-induced vegetation change within these ecotonal grasslands may be soil moisture availability, which, in turn, may be indirectly altered by thermodynamics within the plant canopy and rhizosphere. Plant litter accumulation has been found elsewhere to have an overriding impact on soil moisture content [40] as well as associated diversity responses [18] within Parkland grasslands. Moreover, although species richness had no direct response to our experimental treatments, it

is worth noting that richness was positively related to soil moisture content in both years, suggesting that long-term declines in effective moisture availability, brought about either through reduced precipitation or increased evapotranspiration, may lead to a parallel loss of plant species. This finding is supported by other studies documenting strong effects of interannual variation in precipitation on plant communities [41].

Not surprisingly, light interception was most closely associated with Axis 1 in the NMS from 2006, and directly reflects the prominent impact of leaf area removal during defoliation on the plant community during that year. The negative relationship of diversity with *N* mineralization in 2006 suggests that greater nutrient cycling may lead to a less uniform plant community, potentially due to suppression of those species less adapted to increased *N* availability and an increase in those with favorable responses to *N*. Notably, these results support the work by Dijkstra et al. [42] who documented a more open *N* cycle (i.e., increased soil inorganic *N* and total plant *N*) in a semiarid grassland under warming. Root biomass was also positively associated with *N* mineralization in 2006 and may reflect opportunistic root foraging by plant species adapted to high *N* availability. A common invasive grass of the area, *Poa pratensis* L., is well adapted to *N* addition [43]. Finally, this response during 2006 may also be tied to defoliation in that year, as this disturbance is known to lead to root death of cool temperate grasses in the region [44], which, in turn, would lead to mineralization and the aforementioned increase in nitrophilic species.

5. Conclusions

Despite the short-term nature of this ecological investigation, our results provide useful preliminary information on the initial response of native northern temperate Parkland grasslands to warming and defoliation. Although these grasslands demonstrated prompt but minor changes in diversity and plant species composition in response to warming, these changes disappeared in the second year and were independent of defoliation. Instead, most plant community and biomass responses in this study appeared to depend directly on defoliation and changes to soil moisture availability, light interception, and *N* mineralization, rather than soil temperature. This grassland ecosystem showed resilience to short-term fluctuations in mean annual air temperatures under normal grazing intensities, though long-term impacts require further study.

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References

- [1] R. E. Vance, D. Emerson, and T. Habgood, "A mid-Holocene record of vegetative change in central Alberta," *Canadian Journal of Earth Sciences*, vol. 20, no. 3, pp. 364–376, 1983.
- [2] M. Hirota, C. Nobre, M. D. Oyama, and M. M. C. Bustamante, "The climatic sensitivity of the forest, savanna and forest-savanna transition in tropical South America," *New Phytologist*, vol. 187, no. 3, pp. 707–719, 2010.
- [3] F. Warren, P. Egginton, E. Barrow et al., *From Impacts to Adaptation: Canada in a Changing Climate*, Natural Resources Canada, Earth Sciences Sector, Ottawa, Ontario, Canada, 2007.
- [4] International Panel on Climate Change (IPCC), "Chapter 10: regional climate information—evaluation and projections," in *Climate Change 2001: The Scientific Basis*, J. T. Houghton, Y. Ding, D. J. Griggs, M. Noguer, P. J. Van Der Lindon, and D. Xiaosu, Eds., Cambridge University Press, Cambridge, UK, 2001, Contribution of working group 1 to the 3rd assessment report of the intergovernmental panel on climate change.
- [5] D. S. Lemmen, F. J. Warren, J. Lacroix et al., Eds., *From Impacts to Adaptation: Canada in a Changing Climate 2007*, Government of Canada, Ottawa, Ontario, Canada, 2008.
- [6] S. S. P. Shen, H. Yin, K. Cannon, A. Howard, S. Chetner, and T. R. Karl, "Temporal and spatial changes of the agroclimate in Alberta, Canada, from 1901 to 2002," *Journal of Applied Meteorology*, vol. 44, no. 7, pp. 1090–1105, 2005.
- [7] M. Sankaran, N. P. Hanan, R. J. Scholes et al., "Determinants of woody cover in African savannas," *Nature*, vol. 438, no. 7069, pp. 846–849, 2005.
- [8] D. J. Sauchyn and A. B. Beaudoin, "Recent environmental change in the southwestern Canadian Plains," *Canadian Geographer*, vol. 42, no. 4, pp. 337–353, 1998.
- [9] C. Körner and D. Basler, "Phenology under global warming," *Science*, vol. 327, no. 5972, pp. 1461–1462, 2010.
- [10] M. R. Shaw, E. S. Zavaleta, N. R. Chiariello, E. E. Cleland, H. A. Mooney, and C. B. Field, "Grassland responses to global environmental changes suppressed by elevated CO₂," *Science*, vol. 298, no. 5600, pp. 1987–1990, 2002.
- [11] O. E. Sala, F. S. Chapin, J. J. Armesto et al., "Global biodiversity scenarios for the year 2100," *Science*, vol. 287, no. 5459, pp. 1770–1774, 2000.
- [12] G. C. Trottier, "Disruption of rough fescue, *Festuca hallii*, grassland by livestock grazing in Riding Mountain National Park, Manitoba," *Canadian Field-Naturalist*, vol. 100, pp. 488–495, 1986.
- [13] E. H. Hogg, J. P. Brandt, and M. Michaelian, "Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests," *Canadian Journal of Forest Research*, vol. 38, no. 6, pp. 1373–1384, 2008.
- [14] R. R. Schneider, A. Hamann, D. Farr, X. Wang, and S. Boutin, "Potential effects of climate change on ecosystem distribution in Alberta," *Canadian Journal of Forest Research*, vol. 39, no. 5, pp. 1001–1010, 2009.
- [15] D. H. McCarney, "History of grazing in the Aspen Parkland," *Canadian Journal of Animal Science*, vol. 73, pp. 749–763, 1993.
- [16] H. G. Lund, "Accounting for the world's rangelands," *Rangelands*, vol. 29, no. 1, pp. 3–10, 2007.

- [17] E. S. Deutsch, E. W. Bork, and W. D. Willms, "Soil moisture and plant growth responses to litter and defoliation impacts in Parkland grasslands," *Agriculture, Ecosystems and Environment*, vol. 135, no. 1-2, pp. 1-9, 2010.
- [18] E. G. Lamb, "Direct and indirect control of species richness and evenness by litter, resources, and neighbor biomass in a native grassland," *Ecology*, vol. 89, pp. 216-225, 2008.
- [19] E. Wheaton, S. Kulshreshtha, V. Wittrock, and G. Koshida, "Dry times: hard lessons from the Canadian drought of 2001 and 2002," *Canadian Geographer*, vol. 52, no. 2, pp. 241-262, 2008.
- [20] W. D. Willms, S. Smoliak, and A. W. Bailey, "Herbage production following litter removal on Alberta native grasslands," *Journal of Range Management*, vol. 39, no. 6, pp. 536-540, 1986.
- [21] Environment Canada, "National climate data and information archive," 2008, http://climate.weatheroffice.gc.ca/climate_normals/index_e.html.
- [22] R. T. Coupland and T. C. Brayshaw, "The fescue grassland in Saskatchewan," *Ecology*, vol. 34, pp. 386-405, 1953.
- [23] R. T. Coupland and R. F. Johnson, "Rooting characteristics of native Greenland species in Saskatchewan," *Journal of Ecology*, vol. 53, pp. 475-507, 1965.
- [24] M. D. Coupe, J. N. Stacey, and J. F. Cahill, "Limited effects of above- and belowground insects on community structure and function in a species-rich grassland," *Journal of Vegetation Science*, vol. 20, no. 1, pp. 121-129, 2009.
- [25] E. L. Aronson and S. G. McNulty, "Appropriate experimental ecosystem warming methods by ecosystem, objective, and practicality," *Agricultural and Forest Meteorology*, vol. 149, no. 11, pp. 1791-1799, 2009.
- [26] G. M. Marion, G. H. R. Henry, D. W. Freckman et al., "Open-top designs for manipulating field temperature in high-latitude ecosystems," *Global Change Biology*, vol. 3, no. 1, pp. 20-32, 1997.
- [27] J. A. Klein, J. Harte, and X. Q. Zhao, "Dynamic and complex microclimate responses to warming and grazing manipulations," *Global Change Biology*, vol. 11, no. 9, pp. 1440-1451, 2005.
- [28] E. G. Lamb and J. F. Cahill, "When competition does not matter: grassland diversity and community composition," *American Naturalist*, vol. 171, no. 6, pp. 777-787, 2008.
- [29] C. F. Eno, "Nitrate production in the field by incubating the soil in polyethylene bags," *Soil Science Society of America Journal*, vol. 24, pp. 277-279, 1960.
- [30] B. Attaeian, *Biogeochemical cycling and microbial communities in native grasslands: responses to climate change and defoliation*, Ph.D. thesis, University of Alberta, Alberta, Canada, 2010.
- [31] M. J. Anderson, "A new method for non-parametric multivariate analysis of variance," *Austral Ecology*, vol. 26, no. 1, pp. 32-46, 2001.
- [32] P. W. Mielke, K. J. Berry, and E. S. Johnson, "Multi-response permutation procedures for *a priori* classifications," *Communications in Statistics*, vol. 5, pp. 1409-1424, 1976.
- [33] J. B. Kruskal, "Nonmetric multidimensional scaling: a numerical method," *Psychometrika*, vol. 29, no. 2, pp. 115-129, 1964.
- [34] P. M. Mather, *Computational Methods of Multivariate Analysis in Physical Geography*, John Wiley & Sons, London, UK, 1976.
- [35] M. Dufrene and P. Legendre, "Species assemblages and indicator species: the need for a flexible asymmetrical approach," *Ecological Monographs*, vol. 67, no. 3, pp. 345-366, 1997.
- [36] H. W. Cutforth, B. G. McConkey, R. J. Woodvine, D. G. Smith, P. G. Jefferson, and O. O. Akinremi, "Climate change in the semiarid prairie of southwestern Saskatchewan: late winter-early spring," *Canadian Journal of Plant Science*, vol. 79, no. 3, pp. 343-350, 1999.
- [37] R. T. Coupland, "A reconsideration of grassland classification in the northern great plains of North America," *Journal of Ecology*, vol. 49, pp. 135-167, 1961.
- [38] S. L. Niu and S. Q. Wan, "Warming changes plant competitive hierarchy in a temperate steppe in northern China," *Journal of Plant Ecology*, vol. 1, no. 2, pp. 103-110, 2008.
- [39] R. D. Hollister and K. J. Flaherty, "Above- and below-ground plant biomass response to experimental warming in northern Alaska," *Applied Vegetation Science*, vol. 13, no. 3, pp. 378-387, 2010.
- [40] E. S. Deutsch, E. W. Bork, and W. D. Willms, "Separation of grassland litter and ecosite influences on seasonal soil moisture and plant growth dynamics," *Plant Ecology*, vol. 209, no. 1, pp. 135-145, 2010.
- [41] J. L. Heisler-White, J. M. Blair, E. F. Kelly, K. Harmonay, and A. K. Knapp, "Contingent productivity responses to more extreme rainfall regimes across a grassland biome," *Global Change Biology*, vol. 15, no. 12, pp. 2894-2904, 2009.
- [42] F. A. Dijkstra, D. Blumenthal, J. A. Morgan, E. Pendall, Y. Carrillo, and R. F. Follett, "Contrasting effects of elevated CO₂ and warming on nitrogen cycling in a semiarid grassland," *New Phytologist*, vol. 187, no. 2, pp. 426-437, 2010.
- [43] P. Liancourt, R. M. Callaway, and R. Michalet, "Stress tolerance and competitive-response ability determine the outcome of biotic interactions," *Ecology*, vol. 86, no. 6, pp. 1611-1618, 2005.
- [44] A. Johnston, J. F. Dormaar, and S. Smoliak, "Long-term grazing effects on fescue grassland soils," *Journal of Range Management*, vol. 24, pp. 185-188, 1971.